

MESOSCALE DISTRIBUTION PATTERNS OF QUEEN CONCH (*STROMBUS GIGAS* LINNE) IN EXUMA SOUND, BAHAMAS: LINKS IN RECRUITMENT FROM LARVAE TO FISHERY YIELDS

A. W. STONER,¹ N. MEHTA,² M. RAY-CULP²

¹Northeast Fisheries Science Center

National Marine Fisheries Service

Highlands, New Jersey 07732

²Caribbean Marine Research Center

Vero Beach, Florida 32963

ABSTRACT Populations of benthic species that produce pelagic larvae are sustained through a complex interaction of factors, including larval supply, variable transport mechanisms, and a host of postsettlement processes that affect differential recruitment and abundance. We report distributional data for the larvae, juveniles, adults, and a time-averaged index of fishery yield (shell middens) of the economically important marine gastropod *Strombus gigas* (queen conch) in the Exuma Sound, Bahamas. All life history stages and the fishery yields were heterogeneously distributed around this semiclosed system, with higher densities of benthic stages in the northern part of the sound than in the south and east. Distribution of shell middens closely reflected abundance patterns of shallow-water juvenile aggregations and abundance of adults in depth-stratified surveys; therefore, midden distribution provided a good indicator of long-term productivity around the periphery of the sound. Although patterns of fishery productivity around the system were closely related to both juvenile and adult distributions, and density of newly-hatched larvae reflected the distribution of adults and shell middens, as would be expected, benthic stages and the fishery yields were completely decoupled from the abundance of settlement-stage larvae. When transplants of newly settled conch were made to four seagrass sites in the eastern Exuma Sound with characteristics typical of conch nurseries, low growth rates resulted in all but one location. All of these results suggest that conch abundance and distribution in Exuma Sound is determined in the benthos, either during settlement or in the first year of postsettlement life. Therefore, although larval supply has been shown to influence benthic recruitment on a small scale (i.e., size and location of juvenile aggregations), and juvenile populations will always depend upon a reliable source of competent larvae, high quality habitat plays an equally important role in the recruitment of this important fishery resource.

KEY WORDS: Fishery, habitat, larval supply, mesoscale, oceanography, postsettlement, presettlement, recruitment

INTRODUCTION

Many marine animals have complex life cycles in which they release large quantities of planktonic propagules that are transported by currents to habitats distant from where they were spawned (Doherty and Williams 1988, Roughgarden et al. 1988). Although some marine fishes and invertebrates reduce presettlement losses of larvae by releasing eggs or larvae into transport pathways that favor delivery away from predators and on to appropriate juvenile habitats (Johnson and Hester 1989, Hensley et al. 1994, Morgan and Cristy 1995), the vast majority of these propagules are advected away from suitable settlement habitat, or die during the planktonic or early postsettlement periods. Although all populations that produce pelagic larvae are sustained, to some degree, by the transport of larvae from upstream sources, predation rates on settling and newly settled invertebrates can be very high (Woodin 1976, Osman and Whitlatch 1995, Gosselin and Qian 1997, Stoner et al. 1998), and a host of postsettlement processes can also influence spatial distribution (Hunt and Scheibling 1997). Consequently, the relative importance of pre- and postsettlement processes on distribution has been a subject of much recent research related to invertebrate recruitment (e.g., Olafsson et al. 1994, Eggleston and Armstrong 1995, Wahle and Incze 1997). One way to examine the significance of pre- and postsettlement processes is to test geographic coherence of abundance patterns in all of the life stages, as recommended by Hunt and Schiebling (1997).

The large gastropod mollusk *Strombus gigas* Linne (queen conch) is a convenient model for examining relationships between life history stages for several reasons. First, larvae of *S. gigas* are

readily identifiable at all stages and are relatively large, hatching at about 0.3 mm shell diameter and settling to the benthos at over 1.0 mm in shell length (Davis et al. 1993). Second, juveniles occur in large aggregations, primarily in shallow coastal habitats making them relatively easy to survey. Third, the adults are slow moving, large (to 30 cm), and easily surveyed to their typical depth limit of ~30 m depth. Juvenile and adult conch normally inhabit clear oligotrophic waters, which also facilitates survey work. Fourth, fishers ordinarily land the heavy shells of queen conch on beaches near the collection sites where they extract the edible meat. Because the shells persist on the beaches for at least several hundred years, the shell middens provide an index of historical distribution patterns.

In 1992, the multidisciplinary program FORECAST (Fisheries Oceanography and Recruitment in the Caribbean and Subtropics) was developed at the Caribbean Marine Research Center. The goal of this 5-year program was to provide an understanding of recruitment sufficient to explain mesoscale distribution patterns and interannual variation in economically significant species in Exuma Sound. We have collected distributional data on conch larvae (Stoner and Ray 1996, Stoner et al. 1996a, Stoner and Davis 1997a), juveniles (Stoner et al. 1994, Stoner et al. 1995, Stoner et al. 1996b), adults (Stoner and Schwarte 1994, Stoner and Ray 1996), and shell middens (Stoner 1998) in the Bahamas from as long ago as 1989. In this study, we focus on findings from the FORECAST program related to mesoscale spatial variation in populations of queen conch. We expand our previous analyses of the fishery record and benthic populations to include the entire Exuma Sound system, report new data on synoptic surveys for

queen conch larvae, and investigate patterns of distribution among the interconnected populations of queen conch in this system. We hypothesized that larval production and transport are the dominant factors controlling spatial variation in the distribution of conch larvae, juveniles, and adults in Exuma Sound, and that, as a result, long-term fisheries for conch reflect the general larval supply pattern. We further hypothesized that mesoscale patterns of abundance and distribution may be set during the juvenile stage and mediated by density-dependent postsettlement processes.

Study Site and Background Information

The Exuma Sound is a deep, semienclined basin located in the central Bahamas that extends for 250 km along an axis, oriented southeast to northwest (Fig. 1). It is bordered to the south, west, and north by the Exuma Cays and the shallow Great Bahama Bank, most of which is sand and seagrass habitat less than 4 m deep. Eleuthera and Cat Island bound the eastern edge of the sound. The only deep-water (>200 m) connection to the Atlantic Ocean is at the southeast end of the sound, between Cat Island and Long Island through a pass that is 50-km wide. The pass between Little San Salvador Island and Eleuthera, 16 km wide, is characterized by a sill with depths to approximately 35 m. West of Cat Island a broad island shelf (to 10-km wide) borders the Exuma Sound. This shelf grades slowly from the intertidal through shallow sand and seagrass habitats to sand and coral near the shelf edge in 15 to 30-m depth. The island shelf along the west coast of Eleuthera and the Exuma Cays is narrow (<1-km wide), grading rapidly from the island shores to 30-m depth. The shelf edge begins at 30 to 35-m depth throughout the sound. Steep slopes descend to depths >2,000 m in the southern part of the basin and to near 1,000 m in the northern part. Because the shelf edge provides a curvilinear boundary between shallow-water conch habitats and the deep Exuma

Sound, distance along the shelf edge was used to standardize abundance patterns for juveniles, adults, and shell middens (see below).

The total human population around the periphery of Exuma Sound is <10,000 people, centered primarily in George Town on Great Exuma. As a result, there are few sources of pollution, fishing pressure on queen conch is relatively low, and the ecology of the system is relatively unspoiled. The semienclined nature of the sound and the presence of suitable conch habitat make this system a natural laboratory for the study of fishery recruitment processes and for analysis of distribution of conch from larva to adult.

Along the Exuma Cays, juvenile conch live primarily in seagrass meadows on the shallow bank, and adult conch live primarily offshore in the deeper waters of the sound to 30 m (Stoner and Schwarte 1994, Stoner and Ray 1996). Adult conch lay eggs from April through October (Stoner et al. 1992). The prevailing current on the shelf near the Exuma Cays runs alongshore from the southeast to northwest (Colin 1995) and plays an important role in transporting conch larvae to the northwest. Larvae are advected through the numerous tidal passes between the cays and onto the bank (Stoner and Davis 1997a), where competent larvae settle selectively and metamorphose in nursery grounds that have been well studied (Davis and Stoner 1994). Juveniles live in aggregations at densities of 0.1 to 2 individuals/m² (Stoner and Ray 1993, Stoner et al. 1996a). As they mature into adults, juveniles migrate back through the tidal passes and out to the deepwater reproductive areas (Stoner and Ray 1996). Most conch fishers free-dive for their catch from small boats that have limited range. After removing the meat, they discard the shells along the shores of Exuma Sound, thereby creating ever-growing piles near the site of capture. These piles of discarded shells, hereafter referred to as *middens*, provide a time-averaged record of large-scale conch distribution, and a history of the fishery for at least 500 years (Stoner 1998).

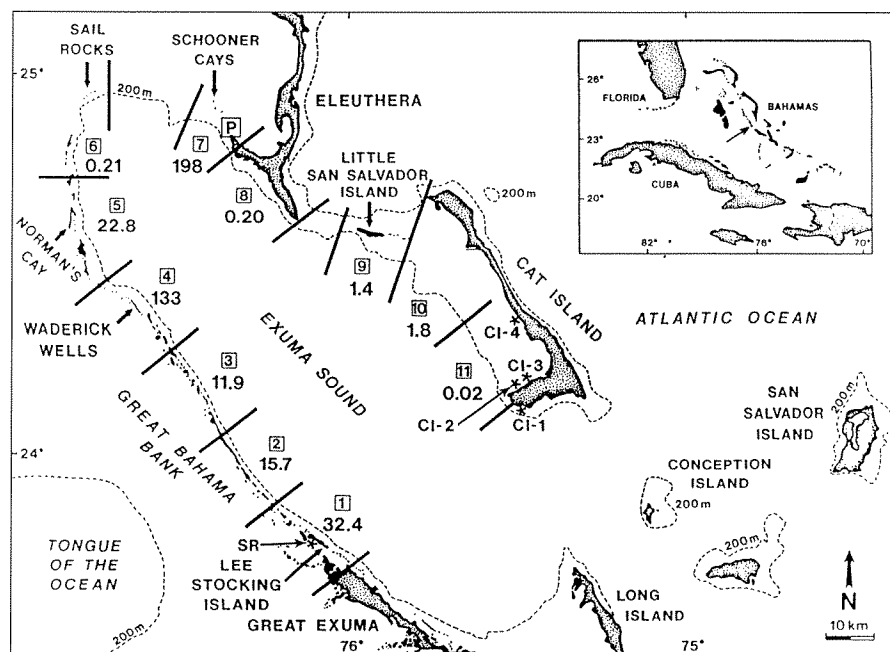


Figure 1. Map of the Exuma Sound system in the central Bahamas. The periphery of the sound was divided into 11 sectors (boxed numbers). The values below the sector numbers indicate the volume of queen conch shell middens expressed in m³ per km of shelf edge (dashed line). Asterisks indicate the five stations at which newly settled conch were transplanted, four at Cat Island (CI-1 to CI-4) and one station at Shark Rock (SR) near Lee Stocking Island. The letter "P" near the island of Eleuthera indicates Powell Point, referred to in the text.

METHODS

Spatial relationships between the abundance of queen conch larvae, juveniles, adults, and discarded shells in middens were examined in and around the Exuma Sound. Surveys for the various life stages spanned several years, and some components of the results, as noted, have been published in previous studies. The methods and results sections will describe the results for different conch stages in reverse ontogenetic order, beginning with middens, because it is this time-integrated spatial record that reflects the long-term fishery that we wish to explain. Furthermore, we were able to quantify shell middens around the entire rim of the Exuma Sound, thereby surveying the entire system. Quantifying all three living conch stages was much more labor intensive, and only regional surveys could be accomplished. A similar survey strategy was used by Lipcius et al. (1997) in an analogous study of spiny lobster (*Panulirus argus*) populations in Exuma Sound.

The purpose of this investigation was not to follow a single cohort of queen conch from larvae to adult stage or to the fishery in the Exuma Sound. Rather, our intent was to examine the long-term record of fishery yields over a relatively large scale (i.e., Exuma Sound) and to interpret it in terms of current abundance patterns observed for early life stages and adults.

Long-Term Record of the Conch Fishery

Shell midden data used in this study were modified from Stoner (1998), where the survey methods were described in detail. Briefly, all of the islands facing the Exuma Sound were searched for shell remains in a clockwise direction from the northern tip of Great Exuma to the southern end of Cat Island between 1989 and 1994 (Fig. 1). The shoreline of Great Exuma was not surveyed, because this island has the largest human population on the periphery of the Sound, and middens have been removed or disturbed by development. Small settlements occur around the rest of the sound, but most of the extensive shoreline is undisturbed.

For this study, the shelf around the sound periphery was divided into sectors that were ~20-km long (Fig. 1). Not included in the division of the periphery were deep-water passes between Cat Island and Long Island, the open-water pass between Little San Salvador and Eleuthera, and the bank periphery where there were no islands for landing conch (i.e., in the extreme northern sound and between Long Island and Great Exuma). Distances were measured at the edge of the shelf and varied somewhat to separate nurseries for queen conch that are associated directly with the tidal flow fields between islands at the edge of the bank (Jones 1996, Stoner et al. 1996b).

Shell middens ranged in size from a few scattered shells to accumulations that were 3 to 4-m high. Estimates of the total volume of individual accumulations were made by measuring their basic dimensions as described by Stoner (1998). Notes were also made on the apparent age of the shell middens. For example, some were composed primarily of very old and eroded shells, and the top layers of others were covered with recently landed shells from which the bright shell nacre had not yet faded. The middens were mapped, volumes were summed for each sector, and the volume of shells per kilometer of shelf periphery was used as a standard index of historic fishery yield from individual bank sectors.

Adult Surveys

Labor-intensive diving surveys for adults were concentrated in four sectors of the sound chosen on the basis of general geographic

positions and known productivity patterns in queen conch revealed in the midden survey. They included: (1) the conch-poor area at the southern end of Cat Island (Fig. 1, sector 11); (2) the well-studied area near Lee Stocking Island in the southern Exuma Cays (sector 1), where conch productivity is moderate; (3) an area inside the Exuma Cays Land and Sea Park near Waderick Wells (sector 4), where Stoner and Ray (1996) found very high densities of adult conch; and (4) an area between the Schooner Cays and the southeast tip of Eleuthera (sector 7), where the highest concentrations of shell middens were located (Stoner 1998).

Stoner (1998) found a positive correlation between middens and juvenile conch abundance, and we hypothesized a similar relationship between middens and adult conch abundance. If such a relationship exists, midden volume could be used as an indicator of living adult conch distribution. Extensive adult surveys were made during the summer 1991 near Lee Stocking Island (Stoner and Schwarte 1994), and near Waderick Wells (Stoner and Ray 1996), Cat Island, and Eleuthera in 1994. Although surveys for conch were made during two different years, the conch populations in the Exuma Sound seem to be relatively stable over the long term. Annual surveys for adult conch conducted at selected sites off Lee Stocking Island between 1988 and 1994 (Stoner and Sandt 1992, unpubl. data) revealed that maximum variation from the mean population size and density was just 19%, and the population was only 4% above average in 1991. This stability is probably a function of low fishing pressure, particularly in depths below the reach of the average free-diving fishers (>10 m), and a queen conch life span of at least 12 years (Coulston et al. 1987).

Depth-stratified surveys for adult conch were conducted in each of the four sectors described above. Seven depth intervals were examined: 0 to 2.5 m (where present), 2.5 to 5 m, 5 to 10 m, 10 to 15 m, 15 to 20 m, 20 to 25 m, and 25 to 30 m. The deepest interval was not surveyed at either Eleuthera or Cat Island because of a very steep grade in depths >25 m that did not seem to support adult conch. The intervals were surveyed along nine offshore transect lines perpendicular to Lee Stocking Island, six lines perpendicular to Waderick Wells, four lines perpendicular to Eleuthera, and three lines perpendicular to Cat Island. Because of extremely low conch densities in the shallow waters (<10 m) near Cat Island, standard swimming transects (described below) were supplemented by extensive observations made by towing one or two divers behind the boat. Densities of approximately zero at most depth intervals (see Results) reflected the results from this more extensive survey method. Total numbers of transects and dives made in each of the four sectors were dependent upon ship time available and logistics. Land-based operations at Lee Stocking Island and Waderick Wells permitted the most intensive surveys.

In each depth interval, two divers swam for 8 to 30 minutes, depending upon depth, holding a taut line (8 m) between them and counting the number of adult conch that lay beneath the line (Stoner and Schwarte 1994, Stoner and Ray 1996). One diver carried a calibrated low-velocity flow meter to calculate the distance traveled. To compensate for the potential influence of current on distance measured, the divers swam into any discernible current and back, covering two parallel, nonoverlapping paths that normally ran parallel to the isobaths. Mean swim distance was 360 m (SD = 106 m), for a typical sampling area of nearly 3 ha. Conch densities were standardized to numbers per hectare. Mean adult conch density was calculated from the replicates at each depth

interval at each sector and then used to generate a final mean representative of that sector for all depths.

Juvenile Surveys

Surveys for juvenile queen conch were conducted in the four sectors of Exuma Sound described above for adults and in sector 5. Juvenile conch in the Exuma Sound region occur in high density (0.1 to 2.0 conch m^{-2}) aggregations and are found almost exclusively in shallow (<5 m-deep) bank habitats (Stoner and Ray 1993, Stoner et al. 1996b). Consequently, aggregations are usually easy to locate in the clear water, but estimations for juvenile abundance require survey techniques different from those used for adults. A detailed description of juvenile mapping technique can be found in Stoner and Ray (1993). In brief, divers were towed systematically over the bank with sufficient intensity to locate aggregations larger than ~ 1.0 ha in surface area. Once located, the boundaries within which density was greater than ~ 0.1 conch m^{-2} were determined and marked with buoys. Buoy positions were then determined using hand-held GPS (Global Positioning System). Aggregations were plotted on a small-scale chart, and their surface areas were determined with a calibrated digitizing board. We made exhaustive surveys for juveniles along known lengths of the shelf edge within each of the five sectors, and surface areas of aggregations were standardized per unit of distance along the shelf (i.e., ha of juvenile aggregation/km of shelf).

In the Exuma Cays, juvenile aggregations were located in shallow seagrass meadows to the west of the islands and were directly associated with flood tidal pathways. They were relatively rare in the high energy, windward (east) side of the islands (Stoner et al. 1996b). On the eastern side of the sound, the western shores of the islands are protected from the prevailing tradewind and wave energy, and juvenile aggregations again occur in shallow seagrass meadows immediately to the west of the islands. Searches for juveniles near Eleuthera were concentrated on the shallow bank areas surrounding the Schooner Cays, and on the open, seagrass-covered shelf adjacent to Powell Point. Because aggregations in this area were very large, they were relatively easy to locate and map. Virtually all of the southern bight of Cat Island and 3 km of the southern shore between the shoreline and 5-m depth was searched by towing divers behind small boats in transects separated by no more than 0.75 km. Many days of towing near Cat Island over the entire length of sector 11 (20 km) produced only scattered juvenile conch and no aggregations. All of the surveys were conducted between 1991 and 1993, depending upon the

availability of ship time and other logistics. The general strategy was to search a section at least 10-km long in each of the five selected geographic sectors (see Table 1).

Veliger Surveys

Plankton surveys for conch larvae were conducted between 1993 and 1995, in an attempt to explain the large-scale distribution of queen conch around the periphery of the Sound. The first survey in 1993 comprised simple transects across the Sound in the southwest to northeast direction. In 1994 and 1995, the surveys were made in conjunction with physical oceanographic studies and were expanded for a more synoptic view of the Sound.

Size-specific larval density data are useful tools for interpreting larval production and understanding transport processes. Early-stage, newly hatched queen conch veligers provide an indication of local larval production, and late-stage veligers (2 to 3 weeks old), which may have originated from a distant reproductive population, yield information on the number of conch available to settle into the benthos (Davis et al. 1993; Stoner et al. 1996a).

Queen conch larvae are relatively easy to sample, because they are photopositive (Barile et al. 1994) and most abundant near the sea surface (<5 -m depth) when conditions are relatively smooth, as is typical during summer in the Bahamas (Stoner and Davis 1997b). All of the plankton samples collected during the surveys described below were made by towing nets in a stepwise oblique fashion from a depth of 5 m to the surface at ~ 1 m/sec during daylight hours (except for a subset of 15 stations sampled during the night in 1994, see below). During the first 2 years (1993 and 1994) collections were made with standard conical nets (diam. = 50 cm, mesh size = 0.202 mm) that collect all queen conch larvae including the smallest (~ 0.3 mm shell length) newly hatched stage. These nets were towed for an average time of 36 minutes, with 12 minutes each at 5 m, at 2.5 m below the surface, and just below the surface. The volume of water sampled, typically 250 to 300 m^3 , was calculated from a calibrated General Oceanics flowmeter suspended in the mouth of the net. Two tows were made at each station.

In 1995, the primary objective was to sample higher volumes of water for late-stage larvae; therefore, net diameter and mesh size were increased to 75 cm and 0.333 mm, respectively. The tow strategy was similar to that used in 1993 and 1994, but total tow time was increased to 45 minutes. Tow volumes with the larger nets were typically 1000 to 1200 m^3 . All plankton samples were preserved in a buffered 5% formalin-seawater mixture.

TABLE 1.
Surface area and concentration of shallow-water juvenile queen conch aggregations in five sectors around the periphery of the Exuma Sound.

Sector No.	General Location	Survey Date	Total Aggregation Area (ha)	Kilometers of Shelf Surveyed	Aggregation Concentration (ha/km)
1	Lee Stocking Island	7/93	129	11	11.7
4	Waderick Wells	2/91	431	17	25.4
5	Norman's Cay	9/91	269	13	20.7
7	Schooner Cays	8/93	650	10	65.0
11	Cat Island	7/93	0	20	0

Juveniles were ≥ 1 year old and were aggregated at densities of 0.1 and 1.0 conch/ m^2 . See Figure 1 for location of each sector.

In 1993, five cruises were made during the peak reproductive season, 12 June to 23 August, on board R/V *Shadow*. During each cruise, a total of 13 stations was sampled along two transects that ran east to west, with one transect across the northern end of Exuma Sound from Waderick Wells to Schooner Cays and the other across the southern sound from Lee Stocking Island to Cat Island (see Results). The four stations at the end of the two transect lines were located in the four sectors that were surveyed for both juvenile and adult conch (sectors 1,4,7,11). The temporal patterns observed during the 1993 plankton surveys (see Results) facilitated the planning of subsequent cruises so that specific larval stages could be targeted, early-stage larvae in the month of June, and late-stage larvae in late August.

In June 1994, two cruises were conducted to provide a synoptic view of veliger density in the Exuma Sound early in the spawning season. On the first cruise (5 to 13 June), 32 stations were sampled from R/V *Sea Diver* along six transects that ran east to west across the sound (see Results). One of the physical oceanographic objectives to be accomplished during this multidisciplinary cruise was the analysis of upper water column circulation. Therefore, 15 stations had to be sampled at night. Although this was not an optimal sampling strategy, Stoner and Davis (1997b) have shown that conch larvae occur in the upper 5 m of the water column during both day and night, under calm conditions. When they occur below 5 m depth, they do so more in response to high wave action and the associated turbulence than to light conditions. On the second cruise (22 to 24 June), 12 additional stations (total of 44) were sampled from R/V *Shadow* at the 20-m isobath along the length of the Exuma Cays (see Results). All samples during this second cruise were collected during daylight hours.

In 1995, two cruises (25 to 31 August and 15 to 17 September) were conducted to obtain a synoptic view of the distribution of late-stage larvae in Exuma Sound during peak settlement period. A total of 41 stations were sampled from R/V *Cyclone* (see Results). The station plan was similar to that employed in 1994, and all collections were made during daytime hours. As mentioned earlier, these collections were made with larger nets and mesh size, to sample late-stage larvae better. Sampling was suspended during a high wind period in early September.

Plankton samples were sorted in their entirety for strombid veligers with the aid of a dissecting microscope. All strombids were identified to species (see Davis et al. 1993, for descriptions), counted, and measured for maximum shell length (SL), but only queen conch veligers (*S. gigas*) are discussed here. The veligers were divided into three general age classes on the basis of size: early-stage (<500 μm SL), midstage (500 to 900 μm SL), and late-stage larvae (>900 μm SL), which were at or near metamorphic competence. Abundance was calculated as numbers of veligers per unit volume of water sampled (veligers/100 m^3) for each age class. Data are reported as the mean of two tows for each station for individual cruises and as mean of means for 1993 when cruises were pooled.

Relationships Among Different Ontogenetic Stages

The abundance and distributional data for middens, adults, juveniles, and larval conch were collected to examine the relationships among distinct ontogenetic stages in different geographic sectors around Exuma Sound. Tests of correlation were performed between conch midden volume and adult conch density, and between midden volume and juvenile conch density. We hypoth-

esized that, if a positive relationship exists between the fishery yield and benthic stages, then midden volume would reflect living adult conch populations and could be used as an index of living conch abundance around Exuma Sound. We also tested the relationship between midden volume and density of early-stage conch veligers along the shelf periphery to determine if newly hatched larvae reflected large-scale distribution of the reproductive stock. To explore the potential importance of larval supply to distribution of benthic populations around the sound, we also tested for correlations between midden volume and density of late-stage larvae and between late-stage larvae and juvenile conch. Individual sectors were often represented by more than one plankton sampling station, providing increased confidence in the values used in the regressions. This varied with year and sampling strategy; however, all plankton stations inside a sector boundary and within 5 km of the shelf edge were included in a mean value.

Transplant Experiment

We observed very low densities of both juvenile and adult conch in the shallow shelf environment at the southern end of Cat Island (see Results). Because late-stage larvae were relatively ubiquitous throughout the sound, it is unlikely that such low density is explained by a low supply of settlement stage larvae to that location. Therefore, we hypothesized that the habitat in this area was unsuitable for juvenile growth and survival. To test this habitat-limitation hypothesis, we conducted a transplant experiment during the summer of 1995 to measure postlarval growth. If the Cat Island habitat was suitable for newly settled conch growth, then postlarvae transplanted there should grow at rates similar to those transplanted in a conch nursery area near Lee Stocking Island called Shark Rock, where a well-studied juvenile aggregation has persisted for over 10 years (Stoner and Waite 1990, Stoner and Ray 1993, Stoner et al. 1994). Although growth rates in enclosures give no indication of predation-induced mortality, they do provide a good index of habitat suitability in terms of food quality and availability (Stoner and Sandt 1991).

Three queen conch egg masses were collected from a reproductive site on the shelf off Lee Stocking Island on 18 June 1995. The eggs hatched 5 days later, and the larvae were cultured according to well-established procedures (Davis 1994). Briefly, larvae were held in 20-L plastic buckets filled with seawater collected daily from the bank west of Lee Stocking Island. Natural foods in the seawater were supplemented with cultured Tahitian *Isochrysis* spp. Metamorphosis was induced on 21 July, at ~1 mm shell length (SL), and postlarvae were raised in plastic trays with aerated seawater on a diet of seagrass detritus (*Thalassia testudinum*) collected from the field.

Five enclosures were deployed at one Shark Rock station in an area of uniform habitat characteristics at a depth of 4.1 m MLW (Fig. 1). It was our intent to deploy the Cat Island enclosures in similar habitat, and, after extensive surveying, four stations were selected along the southwest shore at 3.2–5.3 m depth (Fig. 1). Sediment and seagrass (*Thalassia testudinum*) detritus samples were collected, and living seagrass shoot density was counted near each enclosure to characterize the station (Table 2).

Enclosures were pvc cylinders (diameter = 16 cm, height = 25 cm) with abundant large holes (diameter = 5.5 cm) cut from each to allow for water circulation (after Ray and Stoner 1995). Each cylinder was lined with a polyester mesh (1 mm) sleeve, pushed into the substrata, secured to reinforcement bars driven into

TABLE 2.

Mean growth rate and survival of postlarval queen conch transplanted at four stations near Cat Island (CI) and one station near Lee Stocking Island at Shark Rock (SR).

Station	Growth Rate (mm/day)	Survival (%)	Sediment Type	Seagrass Density (Shoots/m ²)	Seagrass Detritus (g)
CI-1	0.12 ± 0.01 ^a	90 ± 9	Medium sand	570 ± 182	1.35 ± 0.17
CI-2	0.10 ± 0.03 ^a	100 ± 0	Coarse sand	950 ± 178	0.71 ± 0.18
CI-3	0.16 ± 0.01 ^b	90 ± 11	Coarse sand	750 ± 257	0.68 ± 0.28
CI-4	0.30 ± 0.02 ^c	99 ± 2	Medium sand	680 ± 144	0.19 ± 0.13
SR	0.28 ± 0.02 ^c	92 ± 12	Medium sand	710 ± 167	4.51 ± 0.94

Values are mean ± SD; n = 5 at each station except CI-2, where n = 4 for conch growth rate. Growth rate data were homogeneous (Cochran's test, $p > .05$, and differences in the means were determined by one-way ANOVA ($F_{(4,19)} = 114$; $p < .001$) followed by Tukey HSD multiple comparison test. Means that are not significantly different ($p > .05$) are designated by similar lower case letters. Habitat characteristics including sediment type, seagrass (*Thalassia testudinum*) shoot density, and seagrass detrital biomass (dry weight) (n = 5) are also given for each station. See Figure 1 for location of each station.

the sediment, and covered with a mesh top. Large predators were removed prior to introduction of postlarvae.

Prior to transplanting, subsamples of the cultured postlarvae, which were relatively uniform in size, were measured for shell length with dial calipers. Postlarvae were introduced into enclosures (see below) at Shark Rock on 20 August 1995 at 6.0 mm SL (SD = 0.4, n = 40) and at Cat Island on 24 August at 6.1 mm SL (SD = 0.4, n = 80). Each enclosure contained 18 animals.

Postlarvae were recovered from Shark Rock on 9 September, after 20 days in the field, and from Cat Island on 16 September, after 23 days. They were measured for shell length immediately after recovery. Mean daily growth rates were calculated from the living individuals in each cage using the initial shell length from the appropriate subsample. To test for differences among stations, one-way analysis of variance (ANOVA) was performed followed by Tukey HSD multiple comparison test (Day and Quinn 1989).

RESULTS

Long-Term Record of the Conch Fishery

Surveys of shell middens revealed the highly variable nature of the conch fishery yield around Exuma Sound (Fig. 1). Highest shell concentrations (198 m³ shells/km) occurred in the northeast region (sector 7), located between two regions with low concentrations (~0.2 m³/km). A high concentration (133 m³ shells/km) was also observed in sector 4 in the north central Exuma Cays near Waderick Wells. All four sectors in the eastern sound, from Eleuthera to Cat Island, had very low concentrations of conch shells (≤2 m³ shells/km), corroborating the low productivities of conch reported by fishers interviewed at Cat Island. Shells were abundant all along the Exuma Cays island chain on the western boundary of the sound, except at the extreme north.

Most of the shell middens in the Exuma Sound contained both very old and recently collected shells. Important exceptions to this were enormous accumulations of recently collected conch in the vicinity of Powell Point on Eleuthera. These shells had bright color indicating capture over the last few years, and most had the thin shell lips indicative of relatively young adults. The largest individual accumulations (>1000 m³) occurred in sector 4 near Waderick Wells, but it was apparent that most of these shells were collected much earlier than those on Eleuthera. This finding was

not unexpected, because sector 4 lies within the Exuma Cays Land and Sea Park, where all fishing has been prohibited since 1985.

Adult Surveys

In general, densities of adult conch were highest at Waderick Wells and Schooner Cays, intermediate near Lee Stocking Island, and very low (except in the 15 to 20-m depth interval) at Cat Island (Fig. 2). Highest density of adults occurred at 10 to 15 m near Waderick Wells (270 conch/ha), at 15 to 20 m near Lee Stocking Island (88 conch/ha), and at 15 to 20 m off Cat Island (84 conch/ha). Distribution at Schooner Cays was bimodal, with density maxima in shallow water (2.5 to 5 m—228 conch/ha) and in relatively deep water (20 to 25 m—93 conch/ha). Most of the conch in the 2.5 to 5-m interval at Eleuthera were very young adults (with thin shell lips), with a high density of large, late-stage juveniles mixed in as noted below. The adults at most other locations and depths were older.

The benthic habitat within the 0 to 2.5-m depth interval comprised very little surface area in each of the four regions surveyed. Adult conch in this narrow band were rare, and, therefore, considered to be negligible. At all four sites, the two depth intervals between 20 and 30 m represented relatively small proportions of the total habitat occupied by adults; therefore, densities of conch in the depth intervals with largest surface area (2.5 to 20 m) were used to test for correlations between adults and other ontogenetic stages (see below).

Juvenile Surveys

Surveys for juvenile aggregations were conducted in five sectors along the periphery of the Exuma Sound (Table 1). The lengths of shelf edge, corresponding to the shallow-water areas surveyed, ranged from 10 km near the Schooner Cays, where conch juveniles were abundant, to 20 km near Cat Island. Scattered juveniles were observed in the bight of Cat Island and along the westernmost third of the south shore, but no aggregations were found during our extensive systematic surveys conducted in 1993 or during numerous visits to the area between 1993 and 1995. Largest aggregations of juvenile conch occurred in the vicinity of the Schooner Cays just north of Powell Point on the island of Eleuthera and on the shelf immediately west of the Point (Fig. 1), where young adults were also abundant. In August 1993, a single aggregation in the seagrass bed extending south from the Schooner

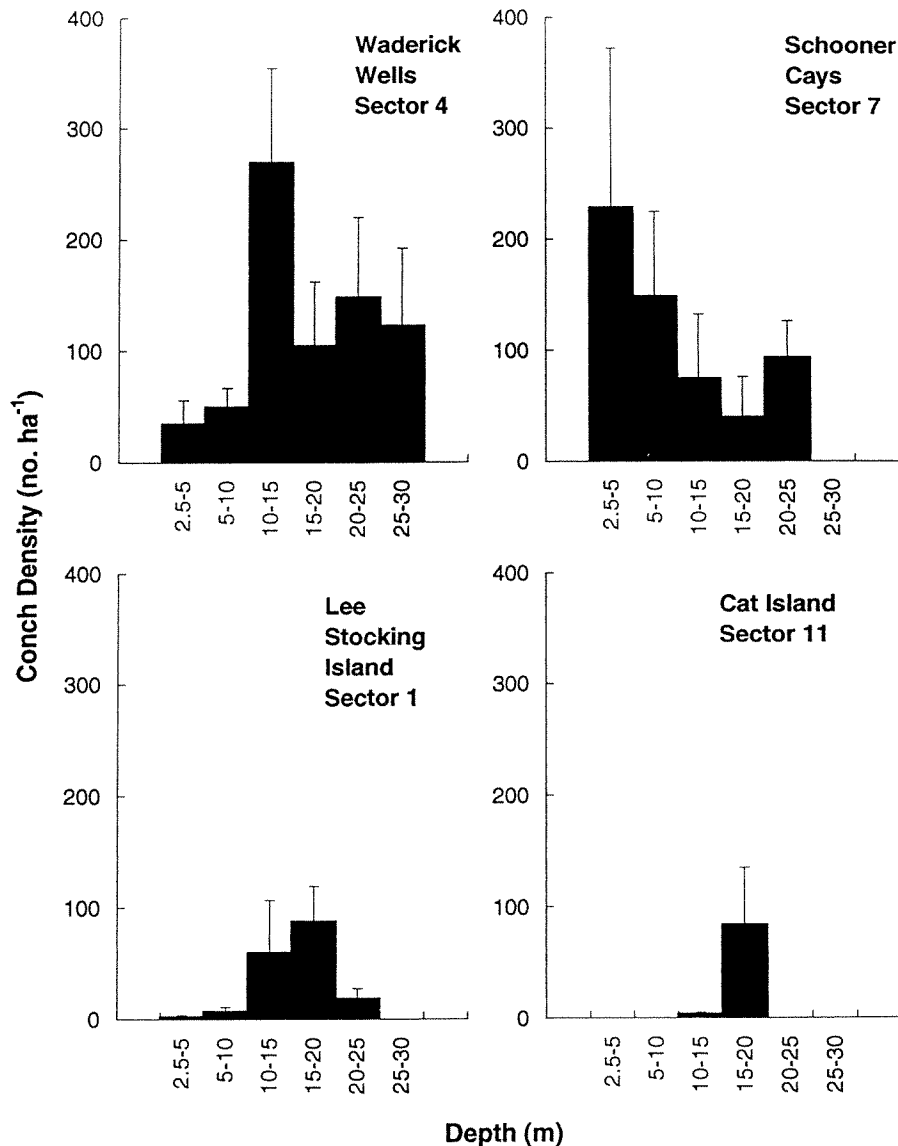


Figure 2. Density of adult queen conch at six depth intervals in the Exuma Sound. Surveys were conducted at four locations, shown here by sector. Values are mean \pm SE. Data for Waderick Wells and Lee Stocking Island are modified from Stoner and Schwarte (1994) and Stoner and Ray (1996).

Cays comprised 610 ha of juvenile conch in densities of at least 0.5 conch/m². Another large aggregation (431 ha) occurred near Waderick Wells. Intermediate concentrations of juvenile aggregations occurred near Norman's Cay (sector 5) in the northern Exuma Cays and near Lee Stocking Island (sector 1) at the southern end of the island chain. Most of the individual aggregations in the Exuma Cays covered between 10 and 100 ha and all were associated with the tidal flow fields immediately west of the inlets and islands in shallow seagrass beds. Repeated observations revealed that the locations of these aggregations were persistent over time.

Veliger Surveys

In 1993, early-stage larvae were most abundant near Waderick Wells (159 to 197 veligers/100 m³), followed by Schooner Cays (29 to 45 veligers/100 m³), Lee Stocking Island (7 to 13 veligers/100 m³), and Cat Island (0 to 5 veligers/100 m³) (Fig. 3A). Early-stage larvae were nearly absent offshore in the open waters of

Exuma Sound. Midstage larvae were concentrated offshore in the northern sound with a mean density of 24 to 41 veligers/100 m³ (Fig. 3B). The mean density of late-stage larvae varied between 0 to 8 veligers/100 m³ at all stations except one offshore in the northern Sound, where mean density was 30 veligers/100 m³ (Fig. 3C). Mid- and late-stage larvae were rarely found along the periphery of the sound during the five surveys conducted in 1993.

As in 1993, early-stage larvae were abundant all along the northern Exuma Cays in 1994, with highest mean densities (208 to 929 veligers/100 m³) near Waderick Wells (Fig. 4A). Stations north of Waderick Wells, near Sail Rocks (see Fig. 1), had mean densities of 65 to 70 veligers/100 m³. The southern part of the sound and the entire eastern periphery yielded low densities of early-stage veligers. For example, Lee Stocking Island, Great Exuma, and Little San Salvador all had intermediate densities of early stages (25 to 59 veligers/100 m³); whereas, Eleuthera and Cat Island had very low densities (0 to 2 veligers/100 m³). As in 1993,

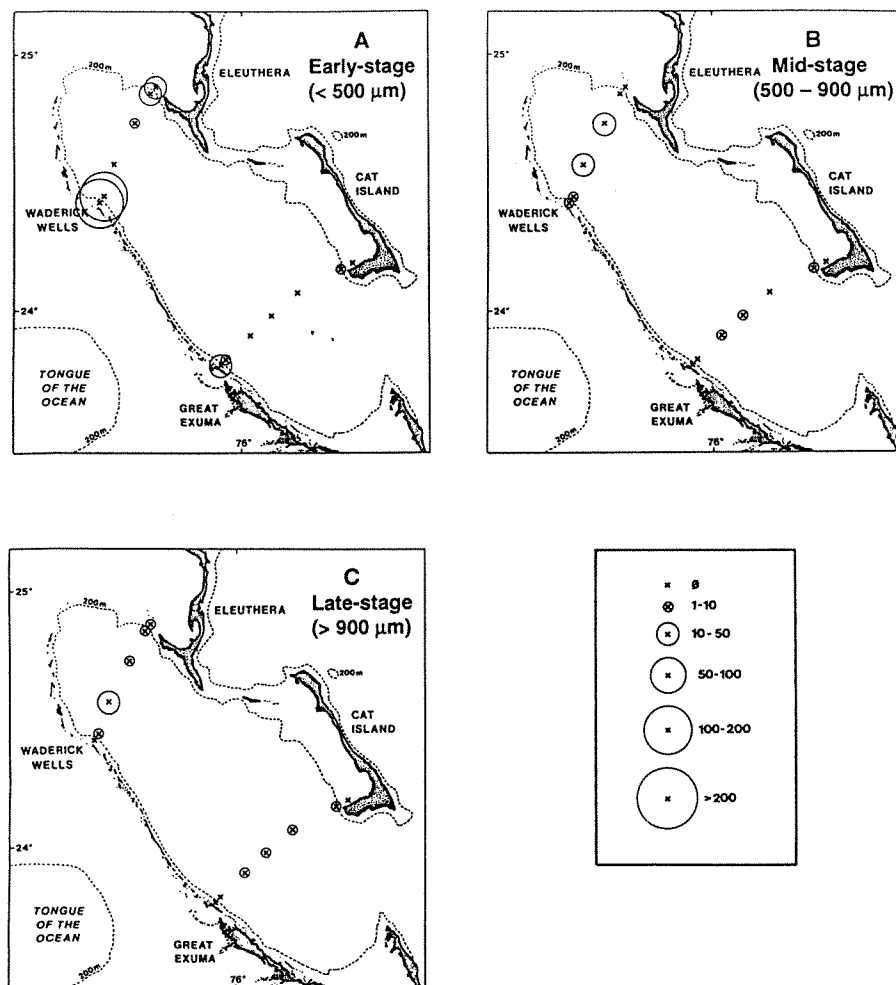


Figure 3. Density of (A) early-stage, (B) midstage, and (C) late-stage queen conch veligers collected during five cruises in 1993 (12 June to 23 August) at 13 stations. Plankton tows were made at each station with 202- μ m mesh nets. Values represent the mean of means for each station.

very few early stages were collected at the offshore, open-water stations.

Although mid- and late-stage larvae were widespread throughout Exuma Sound in 1994, they were usually collected in relatively low densities (Figs. 4B,C). Moderate densities of midstage larvae were found along the shelf edge of the northwest sound near Sail Rocks (45 veligers/100 m^3), near Waderick Wells (24 veligers/100 m^3), and at one station in the center of the Sound (12 veligers/100 m^3) (Fig. 4B). The rest of the sound, including its periphery, yielded a mean density of <10 midstage veligers/100 m^3 . Highest densities of late-stage larvae were found near Sail Rocks (52 veligers/100 m^3), the pass between Eleuthera and Little San Salvador (34 veligers/100 m^3), the outer shelf edge of Cat Island (56 veligers/100 m^3), and one station in the center of the sound (10 veligers/100 m^3) (Fig. 4C). The rest of the sound stations yielded 0 to 6 veligers/100 m^3 . Thus, despite high concentrations of early stage larvae near the large reproductive populations in the north-central Exuma Cays, settlement-stage queen conch larvae were found throughout the sound in relatively low densities.

Veliger distribution was explored along the Exuma Cays in two subsequent cruises, in July and August 1994, and the spatial patterns were remarkably similar to those reported above. For example, highest densities of early-stage larvae were always most

abundant from the middle Exuma Cays to the north, and late-stage larvae were always highest in the extreme northern Exumas.

More intensive surveys for late-stage larvae from late August to mid-September 1995 revealed that these settlement-ready stages were ubiquitous throughout the Exuma Sound, except in the extreme southern sound, in the opening between Cat Island and Long Island, and at numerous stations on the shelf along the Exuma Cays (Fig. 5). Highest densities (10 to 28 veligers/100 m^3) occurred in the extreme northern sound, near Waderick Wells, and at a station south of Little San Salvador. The rest of the Exuma Sound had late-stage densities of 1 to 10 veligers/100 m^3 , with the exception of one station in the central basin (12 veligers/100 m^3).

Relationships Among Different Ontogenetic Stages

When the abundance of shell middens in a sector was compared with the mean density of adult conch on the adjacent shelf <20 m in depth (Sectors 1, 4, 7, and 11), there was a highly significant correlation ($r = 0.973$, $p = .03$) (Fig. 6A). Midden abundance was also closely correlated with the abundance of juveniles in adjacent waters (Sectors 1, 4, 5, 7, and 11) ($r = 0.915$, $p = .03$) (Fig. 6B). The correlations between shell midden volumes and living populations of both juvenile and adult conch

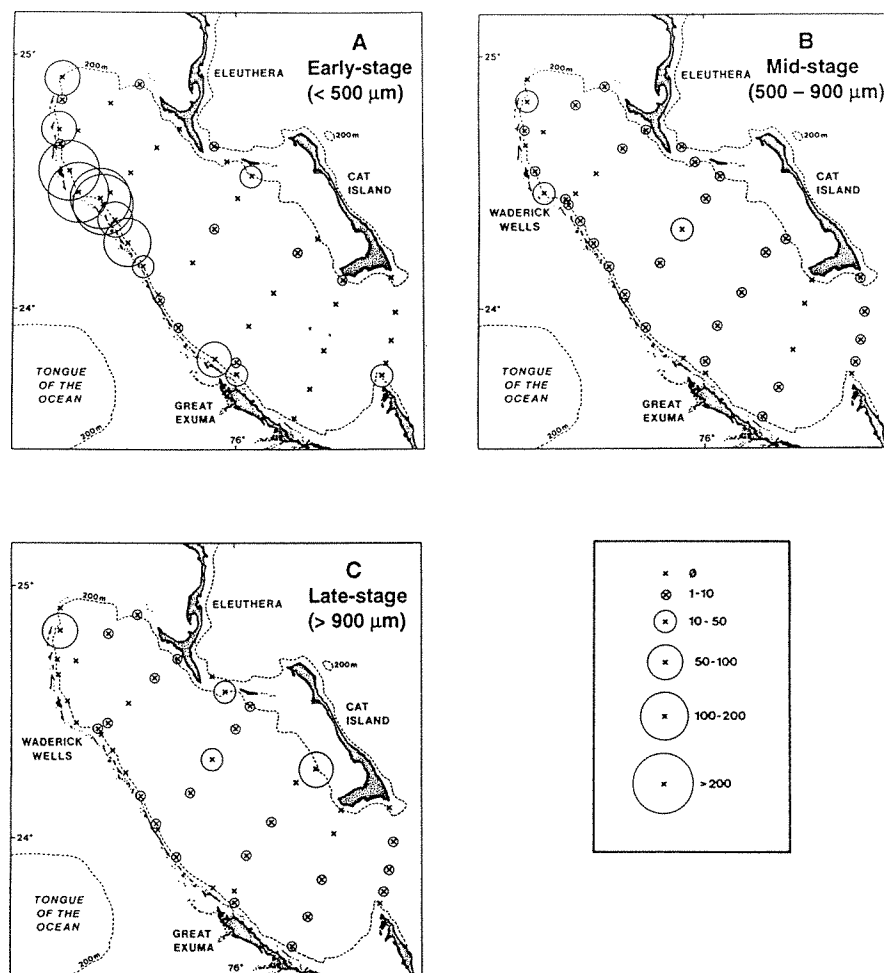


Figure 4. Density of (A) early-stage, (B) midstage, and (C) late-stage queen conch veligers collected during two cruises in 1994 (5 to 13 June, and 22 to 24 June) at 44 stations. Plankton tows were made at each station with 202- μm mesh nets. Values represent the mean for each station.

over the mesoscale validates the use of middens as a proxy indicator of living conch abundance around the perimeter of Exuma Sound.

Abundance of early-stage, newly hatched larvae at any one location should reflect the size and/or density of the reproductive population in the general vicinity. The most synoptic data for early stages were collected in 1994 (Fig. 4), and there were 10 sectors for which we had both veliger and midden data. Very high concentrations of larvae were collected in the north-central Exuma Cays and near Lee Stocking Island in the southern Exumas. Unexpectedly, the correlation between early-stage larval densities and midden abundance was low and not significant ($r = 0.413$, $p = .24$). The poor correlation was a function of one extreme outlier representing sector 7, near the Schooner Cays, where very large populations of adult conch and large middens were found, but few early-stage veligers. As mentioned above, most of the adult conch at this site were very young adults, which may not have been in reproductive state in the summer of 1994. Also, unlike other in-shore shelf stations around the sound, the stations that we sampled for veligers near the Schooner Cays were swept by very strong tidal currents; therefore, it is possible that sampling at this site during the flood tide resulted in low larval densities. The flood tide would carry locally spawned larvae onto the adjacent bank and away from the sampling stations. When sector 7 was removed

from the analysis, there was a highly significant positive correlation between the abundance of early larval stages and middens ($r = 0.964$, $p < .001$), as was predicted. Best distribution of residuals occurred with a natural log transformation of the data ($r = 0.746$, $p = .02$) shown in Figure 7.

We also hypothesized that the juvenile abundance pattern (Table 1) would reflect densities of late-stage larvae (i.e., those that are at or near metamorphic competence and ready to settle). However, using the juvenile abundance data available for five sectors (Table 1), the correlations were low and not significant ($p > .35$) in all 3 years in which larval data were collected ($r = 0.431$ in 1993, $r = 0.512$ in 1994, $r = 0.220$ in 1995) (Fig. 8). In 1994, high densities of late-stage larvae were found at the south end of Cat Island (sector 11) (Fig. 4), where juvenile populations were typically very small. In the same year, sectors with large juvenile populations (e.g., sectors 4 and 5) had low densities of late-stage larvae. In 1995, late-stage larvae were relatively high in sectors 4 and 5, but also common in sector 11 near Cat Island (Fig. 5). Larval supply was not a good predictor of juvenile concentration.

To complete the analysis of the relationship between middens and mesoscale distribution of conch around the Exuma Sound, we examined midden volume as a function of late-stage, competent larvae. The correlations were negative and not significant in 1994 ($r = 0.420$, $p = .23$, $n = 10$) and in 1995 ($r = 0.312$, $p = .35$,

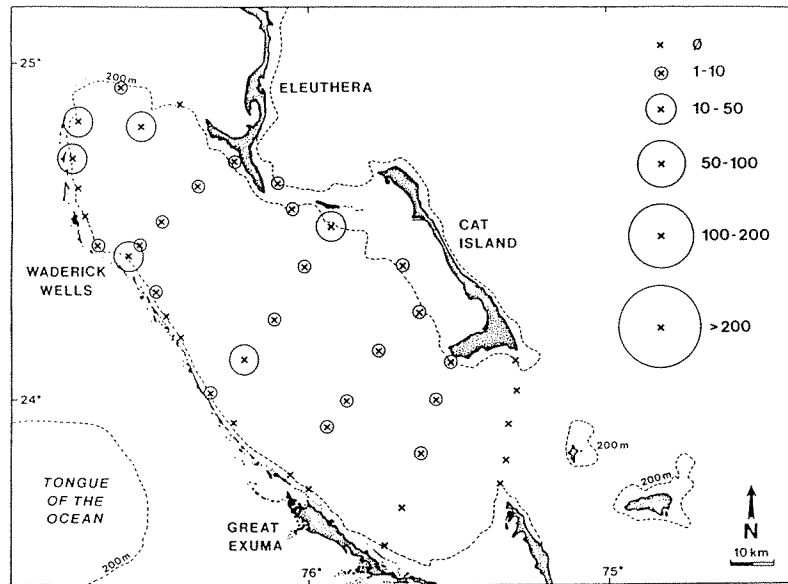


Figure 5. Density of late stage queen conch veligers collected during two cruises in 1995 (25 to 31 August and 15 to 17 September) at 41 stations. Plankton tows were made at each station with 333- μ m mesh nets. Values represent the mean for each station.

$n = 11$) (Fig. 9). As with juvenile distribution, larval supply was not a good predictor for the distribution of fishery yields.

Transplant Experiment

Most (90 to 100%) of the conch transplanted at Cat Island and in the Shark Rock conch nursery were recovered from their enclosures alive, except for one cage at station CI-2, where all conch were lost for unknown reasons (Table 2). Growth rates were significantly higher (0.3 mm/day) at both CI-4 and Shark Rock than at the three other Cat Island stations (0.1 to 0.2 mm/day) (Table 2). Growth was independent of seagrass shoot density and seagrass detritus.

DISCUSSION

It is widely recognized that fishing is better at some locations than others and that this variation occurs over both small and large scales. Variation in the abundance of exploited benthic animals that have pelagic larvae can be explained by differences in: (1) larval supply; (2) larval settlement; (3) the amount and quality of habitat for juveniles; (4) survival to the size at which the animals enter the fishery; and (5) fishing mortality. It is clear that long-term landings of queen conch are not homogeneously distributed around Exuma Sound (Stoner 1998, this study). The purpose of this investigation and the following discussion is to examine the meso-scale patterns of abundance and distribution of all queen conch stages and to determine the point in the life history at which the observed patterns of fishery landings are set.

Radiocarbon dates for shells in middens along the periphery of the Exuma Sound show that these middens provide a historical record of the queen conch fishery spanning several hundred years (Stoner 1998). Although the pattern of conch exploitation is independent of the distribution of human settlements around the sound, there were high correlations between the volume of shell middens and the abundance of both living adults ($r = 0.97$) and juveniles ($r = 0.92$). Thus, midden volumes provide a long-term record of fishing productivity around Exuma Sound as well as an indirect index of living conch distribution. The close correlations between

cumulative landings and local conch populations suggest that the mechanism of distribution occurs somewhere in the life history of conch prior to the age-1 and age-2 year classes that were quantified in the juvenile surveys.

Spatial variation in the adult conch populations was reflected in

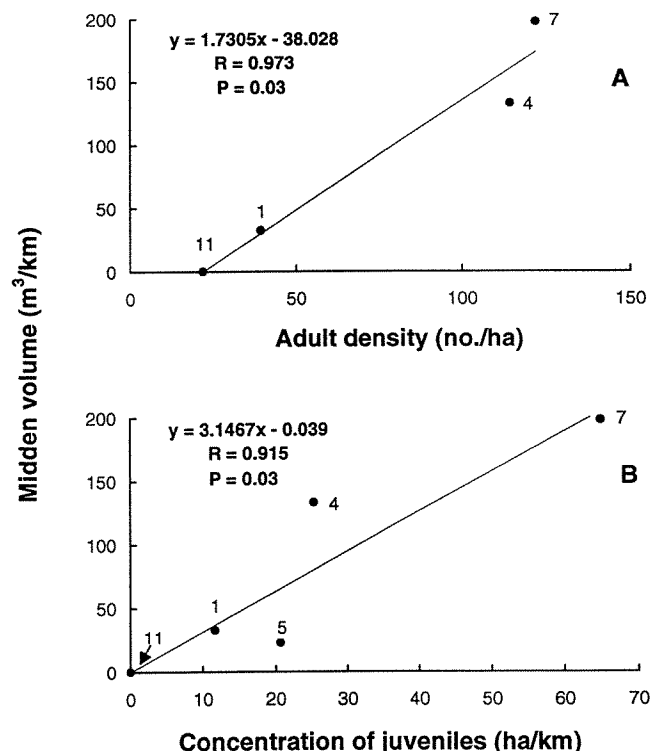


Figure 6. Conch midden volume plotted as a linear function of (A) adult conch density at 2.5 to 20-m depth and (B) concentration of juvenile conch. Pearson correlation coefficients (R) and p -values are given for each regression equation. The number above each point represents the sector at which surveys were conducted in Exuma Sound.

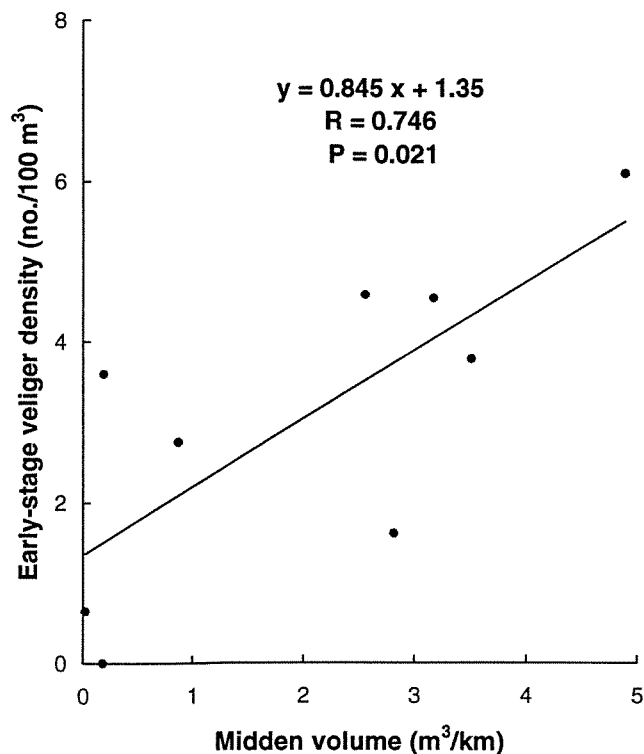


Figure 7. Relationship between mean density of early-stage (<500 µm) conch veligers (natural log transformed) and conch midden volume, surveyed at nine sectors in Exuma Sound in 1994. The Pearson correlation coefficient (R) and p-value are given for the regression equation.

the production of early-stage larvae around the periphery of Exuma Sound. These newly hatched larvae were most abundant in the nearshore areas where adults live and in regions known for high adult concentrations, such as near the Schooner Cays and in the Exuma Cays Land and Sea Park near Waderick Wells. The positive correlation between adults (i.e., spawner abundance) and early-stage larvae was predictable and not surprising.

Ultimately, however, it is settlement-stage larvae that supply and sustain benthic populations, and examples of correlations between larval supply and settlement and/or recruitment to various benthic stages are known for a variety of marine invertebrates (Caffey 1985, Keough, 1988, Bertness et al. 1992) and fishes (Milicich et al. 1992, Doherty and Fowler 1994). Relationships between late-stage larval concentration and juvenile population size have been explored for queen conch in several different locations and on different scales. Stoner and Davis (1997a) have shown that aggregations of juvenile conch were directly associated with local concentrations of late-stage larvae within a tidal current flow field (<10-km long) on the Great Bahama Bank near Lee Stocking Island. Significant positive correlations have also been found between densities of late-stage larvae and juvenile population size on a 10 to 50-km scale across multiple nursery grounds in the Exuma Cays and in the Florida Keys, although the pattern was not coherent across the two locations (~500 km) (Stoner et al. 1996a).

Because of the semiencloded circulation pattern in the Exuma Sound (Colin 1995, Lipcius et al. 1997), it is probable that conch larvae produced in the sound could be retained in the system for the duration of their developmental period. However, the potential

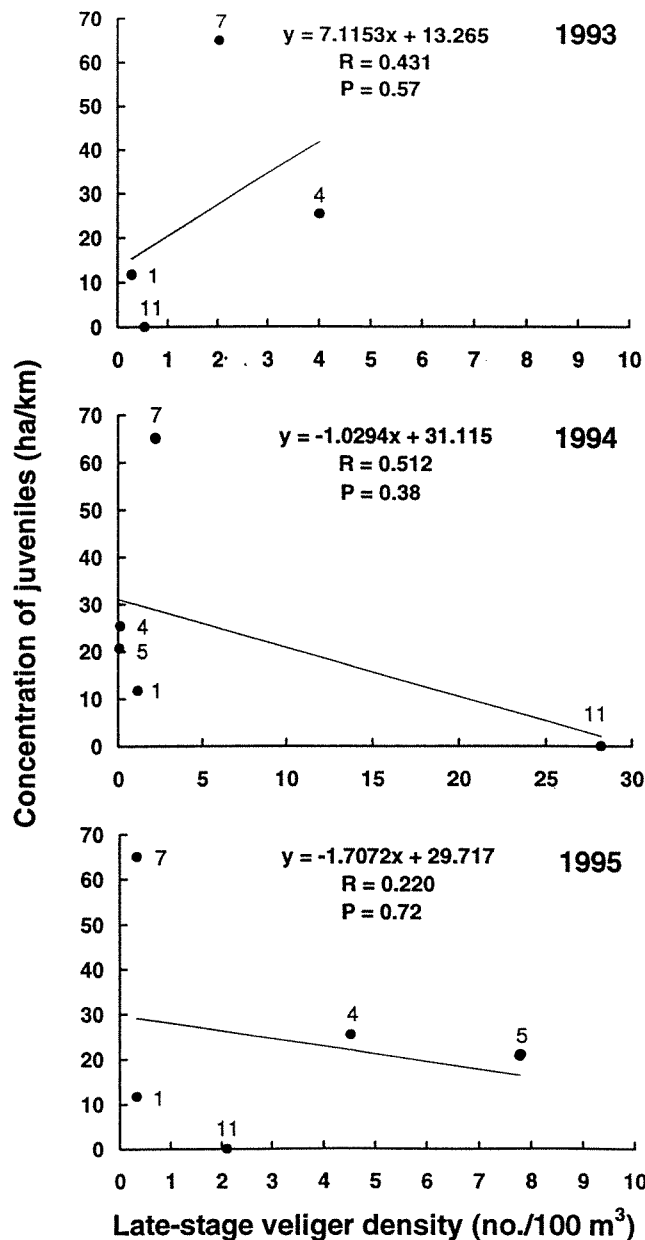


Figure 8. Linear relationship between the concentration of juvenile conch and mean density of late-stage (>900 µm) conch veligers from 1993 to 1995. Pearson correlation coefficients (R) and p-values are given for each regression equation. The number above each point represents the sector at which the survey was conducted in Exuma Sound. Note extended x-axis for 1994 data.

for dispersion within the sound over the 2 to 4 week precompetent period (Davis 1998) is very large. Although late-stage conch larvae were consistently abundant in the northern Exuma Sound during 1994 and 1995, they were relatively ubiquitous throughout the sound. Correlations between the concentrations of settlement-stage larvae and either juvenile or midden distributions were never significant in any of the 3 survey years despite consistent spatial patterns of larval density. These results suggest that the regional pattern of distribution in benthic life stages within Exuma Sound is set by settlement processes and/or early postsettlement processes during the first year of life, and not by differences in larval supply. Lipcius et al. (1997) arrived at similar conclusions about the large-

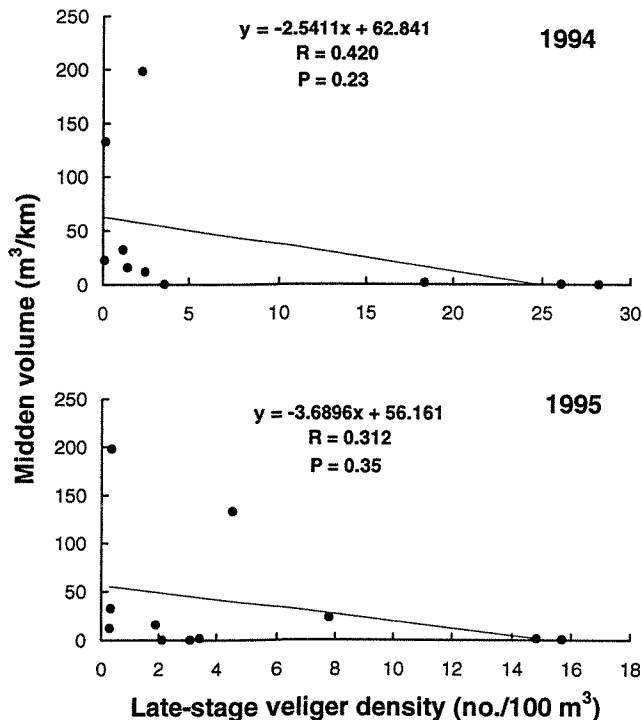


Figure 9. Linear relationship between queen conch midden volume and mean density of late-stage ($>900 \mu\text{m}$) conch veligers in 1994 and 1995. Pearson correlation coefficients (R) and p -values are given for each regression equation. Symbols represent sectors surveyed in Exuma Sound for the 2 years.

scale distribution of spiny lobster (*Panulirus argus*) populations in Exuma Sound. Settlement stage lobster were abundant at Cat Island, yet benthic populations were small. The decoupling between larval supply and juvenile and adult stages was attributed to habitat limitation for early juvenile lobster at Cat Island.

Miron et al. (1995) pointed out the inherent methodological difficulties in correlating larval supply and larval settlement or recruitment. They noted that competent larvae must be quantified and that they must be sampled properly (i.e., with proper respect to location in the water column and settlement substratum). Although settlement-stage queen conch larvae have never been collected in high densities, compared with densities of other mollusks in temperate waters, they are relatively easy to sample, because they occupy near-surface waters in most circumstances (Barile et al. 1994, Stoner and Davis 1997a, Noyes 1996). Furthermore, it is relatively easy to identify competent forms on the basis of size, pigmentation, and other features (Davis 1998). Consequently, we believe that we have sampled the correct larval stages using an appropriate technique.

It can also be argued that larval supply is best measured as a rate of delivery of competent larvae to a potential settlement site (Olmi et al. 1990, Yund et al. 1991). Measuring this is particularly difficult for queen conch on the Great Bahama Bank because of strong tidal currents (see Stoner and Davis 1997b). However, the difficulty is lower in the Exuma Sound, and we have high confidence in the regional patterns of larval abundance reported for two reasons. First, currents in the sound are much weaker ($<20 \text{ cm/sec}$; Colin 1995), than those on the Bank (often $>100 \text{ cm/sec}$; N. P. Smith, unpubl. data), so the issue of larval flux is less complicated in the sound than on the nursery grounds of the Bank. Second, and

more importantly, multiple visits to selected stations throughout the sound between 1993 and 1994 revealed that the regional patterns in veliger distribution were consistent over time. For example, five cruises over 13 stations in 1993 showed that early- and midstage larvae were always abundant in the northern sound, and always highest on the shelf adjacent to Waderick Wells. Late-stage larvae were always most abundant in the sound offshore from Waderick Wells. Three cruises along the island shelf east of the Exuma Cays in 1994 (Stoner and Mehta, unpubl. data) confirmed the pattern of maximum abundance of early- and midstage larvae in the vicinity of Waderick Wells and to the north, and late-stages were most abundant near Sail Rocks in every case. Larvae of all stages were always rare in the extreme south section of the sound. Therefore, because of the consistency of larval distribution, both within and between years, we believe that the regional patterns of larval abundance reported in this study are representative for the sound.

Given that the abundance of late-stage larvae did not explain mesoscale variation in the abundance of juveniles, adults, or fishery yields of queen conch in the Exuma Sound, we conclude that the regional distribution of benthic stages is regulated by settlement and/or postsettlement processes associated with some element of the habitat. Similar conclusions have been drawn for a large number of other marine invertebrates (Keough and Downes 1982, Luckenbach 1984, Connell 1985, McGuinness and Davis 1989, Osman et al. 1992, Olafsson et al. 1994, Eggleston and Armstrong 1995, Hunt and Scheibling 1997, Lipcius et al. 1997).

Many invertebrates settle and metamorphose in the presence of certain chemical agents in or on the substratum (Morse and Morse 1984, Hadfield and Scheuer 1985, Burke 1986, Butman and Grassle 1992, Pawlik 1992), and Mianmanus (1988) has shown that phycobiliproteins associated with red algae are active agents in conch settlement and metamorphosis. We know from extensive dredge sampling for newly settled queen conch (both live and recently killed) in a tidal flow field near Lee Stocking Island that settlement is not random and that it occurs in specific locations (Stoner et al. 1998). This confirms earlier laboratory experiments showing that competent queen conch larvae settle in response to specific biological cues found within nursery grounds (Davis and Stoner 1994). Queen conch larvae are, in fact, capable of testing the substratum, returning to the water column multiple times, and delaying metamorphosis for long periods of time (for at least 60 days after competence is achieved) (Noyes 1996). Experimental laboratory work shows that the larvae settle and metamorphose only in habitats where subsequent growth rates are high (Stoner et al. 1996c). Consequently, it is possible that variation in the abundance of queen conch populations on the Great Bahama Bank surrounding the Exuma Sound is related to either the quality or quantity of habitat with appropriate settlement cues and high growth potential for postlarvae.

Habitat-limitation is the most plausible explanation for the low abundance of juvenile and adult conch west of Cat Island, because competent larvae were present in substantial numbers. Frequency of settlement was not tested, because the only way to ascertain this is by dredging, which is extremely labor intensive. However, transplant experiments provide important insights into the nutritional quality of potential nursery sites. Two lines of reasoning suggest that habitat at Cat Island is limiting for conch. First, the type of habitat that typically supports juvenile conch on the Great Bahama Bank (moderate density seagrass with accumulations of decomposing detritus and red and green algae) has been studied exten-

sively (see Stoner 1997), and was uncommon on the bank west of Cat Island. Seagrass was found in relatively small patches (1 to 10 ha), and much of this was exposed to higher physical energy than is typical for conch nurseries. Second, only one of the four sites assumed to be suitable for juvenile conch provided for growth rates similar to those in a known nursery near Lee Stocking Island. Therefore, it is likely that the small queen conch population and the poor fishery for conch near Cat Island is habitat-limited.

Differential mortality of young conch could also explain regional variation in recruitment to the age-1 year class. There are a host of predators on juvenile conch (Randall 1964), including a large variety of recently discovered micropredators such as xanthid crabs and certain polychaetes that feed on newly settled conch (Ray-Culp et al. 1997). It is now recognized that mortality rates in newly settled invertebrates can be very high (Osman and Whitlatch 1995, Gosselin and Qian 1997), and queen conch are no exception (Ray et al. 1994, Stoner and Glazer 1998). Although we did not test for regional variation in mortality of juvenile conch, this is a possible explanation for the population patterns observed.

Conclusions and Fishery Management Implications

Genetic analysis of queen conch collected from 22 populations throughout the greater Caribbean region, including the Bahamas and south Florida indicate a high rate of gene flow among the populations (Mitton et al. 1989, Campton et al. 1992), and certain populations may depend entirely upon upstream reproductive sources (Stoner et al. 1997c). It is clear, therefore, that sound fisheries management will demand good knowledge of larval drift and associated metapopulation dynamics (Berg and Olsen 1989, Appeldoorn 1994, Stoner 1997). However, the direct correlation between the quantity of larvae supplied to the nurseries and the

subsequent abundance of juvenile queen conch in the benthic population that occurs at a local scale (Stoner et al. 1996a) seems to break down at the large scale. In Exuma Sound (180-km long) the abundance of early-stage larvae was positively correlated with regional abundance of adults. However, the distribution of juveniles, adults, and fishery yields was independent of the abundance of competent larvae, and processes of settlement and postsettlement seem to regulate benthic population size. We have shown in the past that conch nursery grounds have unique physical and biological features that enhance larval settlement, provide high nutritional qualities, and promote high survivorship (Stoner et al. 1995, Stoner 1997). It is now clear that high abundance of competent larvae does not guarantee high queen conch production, and that fisheries management for the species must consider both qualitative and quantitative elements of habitat for young conch. Because vast shallow-water areas within the biogeographic range of queen conch are, in fact, not suitable for production of the species, both local- and large-scale mechanisms of population dynamics and habitat use need to be understood, and the ecological integrity of key nursery habitats needs to be preserved.

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